

Studies on Pakistan Reptiles. Pt. 3. *Calotes versicolor*

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Abstract: -Variation in the scutellation and color of *Calotes versicolor* populations in Pakistan are analyzed, leading to the recognition of a new subspecies (*C. v. nigrigularis*) from the front ranges of the Himalayan Mountain complex in Afghanistan, Pakistan and India. Several variant populations of the same species in other parts of its range are noted, but not given taxonomic recognition at this time.

Key words: Reptilia; Sauria; Lacertilia; Agamidae; *Calotes*

Introduction

Calotes versicolor, a large, common, widespread and showy lizard, was described early in the history of reptilian study in the Indian subcontinent (Daudin 1802, as *Agama versicolor*, type loc. "India", restricted to near Pondicherry, India by Kuhl 1820). Variation in color and scalation was also documented early, resulting in the description of several species (now synonyms, see Smith 1935 for review) and races. No subspecies are recognized at the present time, in spite of obvious geographic variation and a wide ecologic and geographic range.). The current study of color and scalation supports the contention of earlier workers that morphologically distinct populations with circumscribed geographic boundaries exist. The latest morphological study is by Tiwari and Aurofilio (1990), though it is restricted to populations from Tamil Nadu, India.

During the collection of new material for a future major publication on the herpetology of Pakistan, populations of *Calotes versicolor* from the mountains of northern Pakistan were noted as being distinctly different from those in other parts of the country. This discovery suggested an analysis of geographic and sexual variation in several scute and color characters, similar to our earlier study of Pakistan *Echis carinatus* populations (Auffenberg and Rehman 1991). The following is the result of this analysis.

Methods

This study is based on slightly more than 500 specimens located in the 14 institutions listed below. The museum source of those specimens specifically referred to are identified by the abbreviations given.

American Museum of Natural History, New York (AMNH); Natural History Museum, London (BMNH); Bombay Natural History Society (BNHS); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Harvard University (MCZ); Pakistan Museum of Natural History, Islamabad (PMNH); Senckenberg Museum, Frankfurt (SMF); Florida Museum of Natural History, University of Florida (FMNH/UF); University of Michigan Museum of Zoology, University of Michigan (UMMZ); National Museum of Natural History, Washington (USNM); Zoological Survey Department, Karachi (ZSD); Zoological Survey of India, Calcutta (ZSI) and Alexander Koenig Museum, Bonn (ZFMK).

All drawings were done by the senior author.

Figure 1 shows the localities from which specimens were examined. Appendix 1 provides data on museum holdings of specimens examined from these geographic locations. No specimens with either general, questionable, or erroneous locality

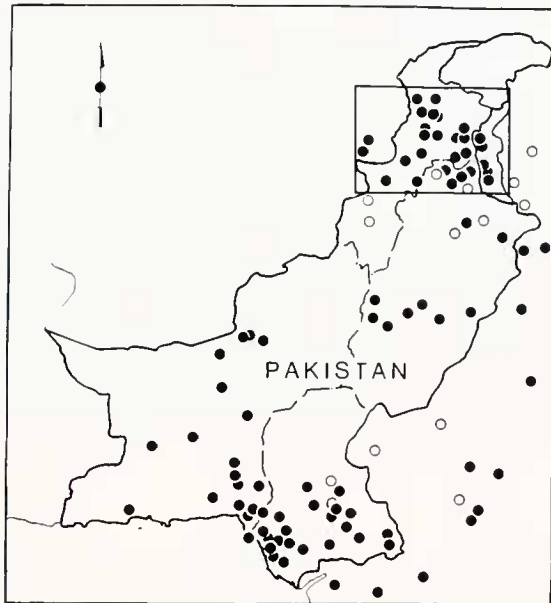


FIG. 1. Localities in Pakistan and adjacent countries from which we examined specimens (dots). Pakistan localities for which we know material is available in museums, but which we have not seen are indicated by circles. The area represented in Fig. 9 is shown with a rectangle.

data have been included. All data used in the analyses were obtained by us - none were drawn from the literature.

The following characters were tabulated for all the specimens listed above: 1) number of subdigital laminae under toe IV, 2) number of scale rows at midbody, 3) snout-vent length (SVL), 4) degree of mucronation of dorsal scales (0 none or very weak, 1 moderate mucronation, 2 strong mucronation; Figure 2), 5) angle of posterior edge of dorsal scale rows (Fig. 3), 6) number of gular scales from just behind mental to a level even with the middle of the eye, 7) number of scales in the dorsal crest that are higher than the length of their base, 8) color pattern of chin, 9) color pattern of belly, 10) color pattern of dorsal body surface, 11) degree of darkening of postorbital stripe (0 none, 1 moderately dark, 2 very noticeable, see Figs. 9, 12), and sex.

Figure 4 shows the locations and general size of sample areas chosen. The geographic limits of the samples were

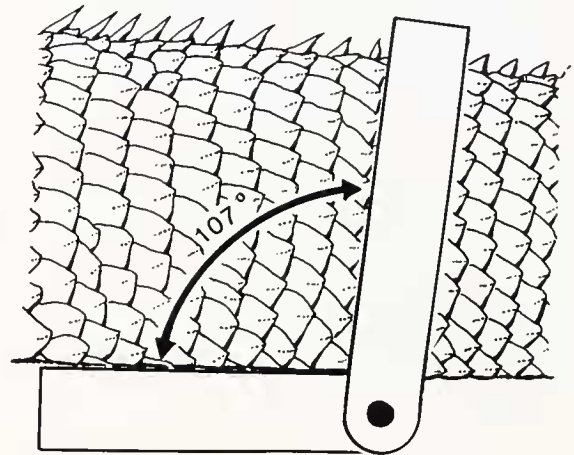


FIG. 2. Side of body of *Calotes versicolor*, showing method of determining the angle of the dorsal scale rows.

selected principally on the basis of sample size (museum material available), but in some cases partly on environmental differences between closely approximated geographic areas (i.e., elevation, major habitat, etc.). Each of these sample areas served as the basis for all calculations and evaluations, so that all specimens available from each area were considered as constituting the same sample for computational purposes.

Results

Only one species of *Calotes* - *C. versicolor* - has been identified by us in Pakistan, though two others were previously listed or implied as occurring there. Murray 1886 reports *Calotes grandisquamis* (Gunther 1875, a valid species from southern India) from Sindh Province (Karachi and Jerruck), Pakistan. There are no substantiating specimens and none of the several herpetologists who have worked in the Karachi area for extensive periods since have ever found this species. It is distinctly different from *C. versicolor* in its decidedly green body color, the significantly lower number of transverse midbody scale rows (27-35), and in the presence of a short, oblique fold (sometimes called a pit) in front of the shoulder.

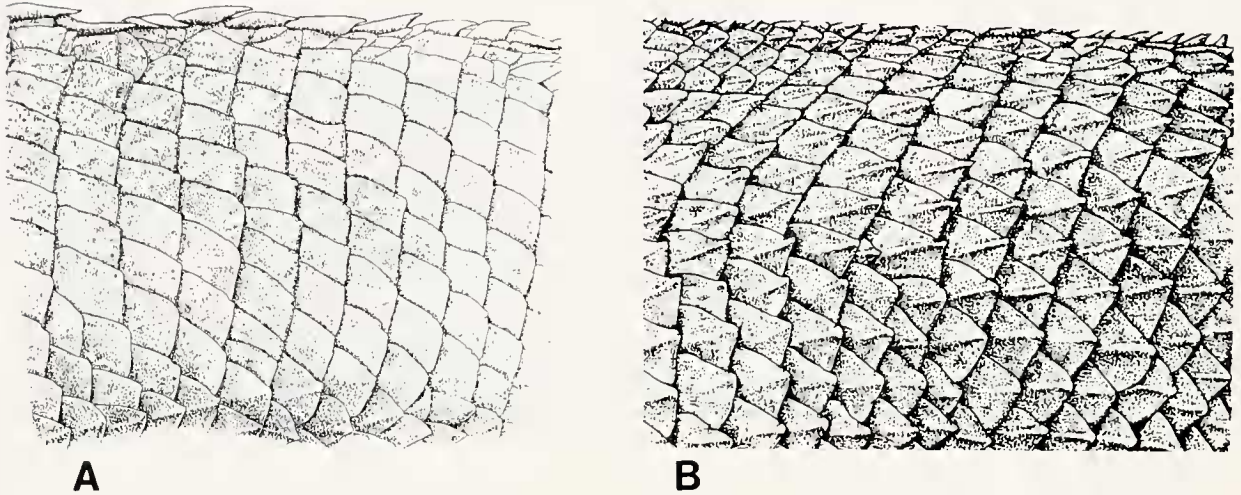


FIG. 3. Geographic variation in degree of lateral body scale mucronation. A, *Calotes v. versicolor*, FMNH/UF 70516, adult male, Karachi, Karachi Dist., Sindh Prov., Pakistan..

The second species is *Calotes jerdoni* (Günther 1870, type loc. Khasi Hills, Assam, India. It is represented in the BMNH by two preserved specimens cited by Boulenger 1885), said to have been taken in Afghanistan. This locality suggests that the species should also be found in the intervening Pakistan area. The Afghanistan data are obviously incorrect, as has already been suggested by Smith (1935). *Calotes jerdoni*. We have examined the specimen in question and confirm it belongs to this species, which is easily distinguished from *C. versicolor* on the basis of its bright green color and the parallel rows of enlarged and keeled scales on top of the head, and in lacking the characteristic pair (usually) of enlarged spines above the tympanum.

We believe that *Calotes versicolor* is the only species of the genus in Pakistan. Between populations of this species in and beyond the borders of Pakistan we are able to demonstrate significant clinal variation (north/south, east/west) beyond that ascribable to race. Such clines occur in at least four scale characters. Sexual variation is demonstrated in color and adult size.

Within Pakistan boundaries, geographic variation suggests the recognition of two races of *Calotes versicolor*, one of which is new. It is described below. Additionally, the populations found essentially east of

India are distinguished on the basis of color and scale characters. However, in this paper we do not recognize them as separate nomenclatorial entities. The solution to the question of their status must await the availability of additional, fresher material.

Individual And Geographic Variation

Here we discuss the variations in color, proportion, and scutellation which are correlated with geographic locality, sex, environment, or ontogeny.

Clinal Variation

The term cline has been used to express a condition in which the values of a variable character form a slope or gradient over a geographic area. With increasing knowledge of variation systematists have come to recognize different types of clines. Some are related to gradual changes in environment (including climate) and others are not. The change in character state over distance have varying slopes when the values of the characters being examined are plotted against distance. Two extreme types of clines are recognizable - *narrow* (or steep) and *broad* (or low) slopes. The former is represented by a character-gradient which significantly changes its slope in a step-like fashion, with separate subspecies corresponding to two more or less level character values (flat or slightly



FIG. 4. Location, size, and approximate area of samples used in this study

sloping) on either side of a uniting steeper slope - the zone of character intergradation. The broad cline is one which does not show any steepening of the character gradient in a particular place, but is represented by a continuous slope with no obvious interruptions. There are, of course, all gradations of slope between these two extreme types. Both narrow and broad clines, as well as intermediate types, exist within the pattern of character variation in the species *Calotes versicolor*.

Number of midbody scale rows (Fig. 5). —The mean number of midbody scale rows illustrate the narrow type of clinal character change in which there is a distinct and rapid change (= steep slope) from one rather uniform area to another. In *Calotes versicolor* a steep north-south cline exists between the northern Himalayan Mountain and Indo-Gangetic Plain populations. The mean dorsal scale rows of all southern (plains) populations (India and Pakistan combined) is 43.0 ± 1.0 (OR sample means 41.0-44.1); for all northern (upland) populations (India, Pakistan, Afghanistan, Nepal) the mean is 45.9 ± 1.5 (OR sample means 43.0-49.2). The difference in mean number of dorsal scale rows between northern and southern populations is

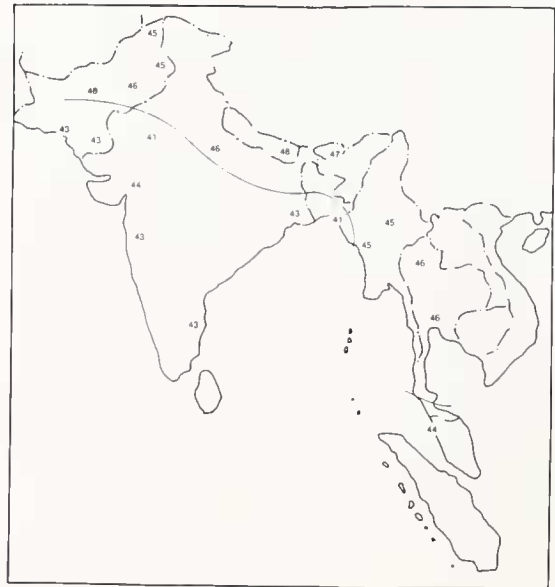


FIG. 5. Geographic variation in mean number of dorsal scale rows of *Calotes versicolor* samples studied. Lines (isophenes) enclose samples of similar value (see text).

highly significant (t 5.83, df 13, $p < 0.001$), with the distinct change in slope of the character gradient occurring along the frontal hills of the northern and northwestern mountains of Pakistan. Similar north-south clines can be demonstrated within this species in other characters as well (see below). However, there is no significant east-west change in the mean character state value in either the plains or the mountain populations, in spite of the fact that other character states do show important east-west changes (see below). Thus the east-west axis of the pattern of character change is independent of the north-south axis. Within southern, plains populations, several samples have graphically different values for this character than all the surrounding ones (Quetta is higher, Rajasthan and the Mekkran Coast are lower). However, in every case, the samples from these sites are small and the differences are not statistically significant.

Subdigital lamellae under 4th Toe (Fig. 6). —In this character the pattern of geographic variation is more complex. There is no clear north-south trend. While

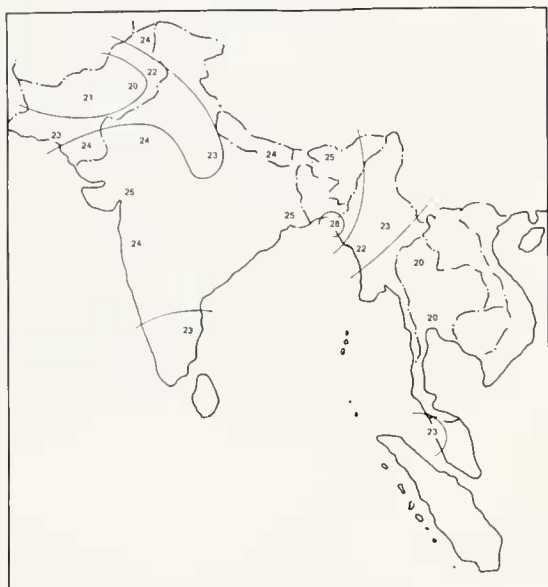


FIG. 6. Geographic variation in the mean number of lamellae under the 4th toe.

equally high values occur in the upland, northwestern part of the species range, the same isophene sweeps down to sea level in the Calcutta area, terminating in the high value for Chittagong (though the latter is statistically insignificant). This tongue of higher values separates the Myanmar-Malaysian populations in the east from the Indo-Pakistan ones in the west. Within Pakistan there is no clear evidence of the even clinal changes witnessed in the mean number of dorsal scale rows (the difference in means between eastern and western Mekkran populations is based on small samples and is statistically insignificant). Thus the overall pattern of character change is one of an east-west component in which geographically intermediate populations (West Bengal) have distinctly higher mean values than populations to both the east and west. At the same time, the "isolated" eastern section includes a population in Thailand in which the mean value (low) is statistically distinct from its neighbors (with Arakan t 3.23, p < 0.01; Rangoon t 2.70, p 0.02; Penang t 3.56, p 0.001). Near the western edge of the species range there is an apparent north-south trend, in which the former area (Jalalabad, Peshawar and Taxila combined) has a statistically significant higher mean value than the south

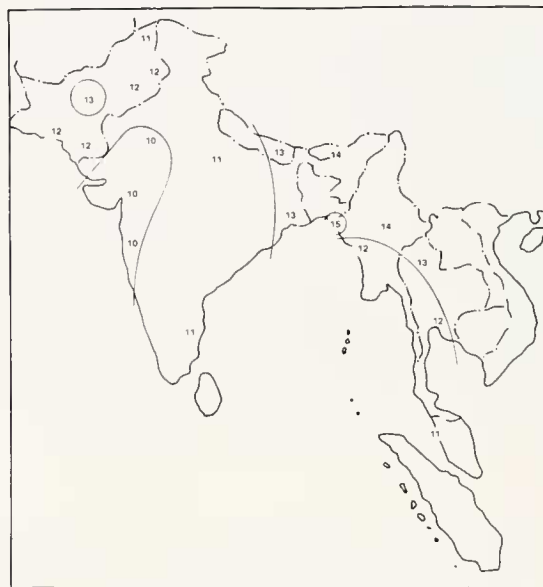


FIG. 7. Geographic variation in the mean number of gular scales.

(Baluchistan) ones (t 3.15 p 0.01). This pattern is, however, confused by populations from Azad Kashmir and Swat District, which are more like one another in having statistically similar low mean values than either is to populations from the geographically intermediate area of Manshera District.

Number of Gular Scales (Fig. 7). —In this character there is a distinct two-way, east-west cline which proceeds from lowest mean values in peninsular India to higher values to the west (reaching maximum values in those samples in the arid mountains at the eastern edge of the Iranian Plateau) and the east (highest in Chittagong and Mandalay). There is no evidence for a north-south cline anywhere. The Chittagong sample is again distinctive (though sample size is small and the values are not significantly different from neighboring ones).

Angle of Dorsal Scale Rows (Fig. 8). —This character illustrates still another clinal pattern—essentially northwest to southeast. Highest mean values (111-119) are found in the former and lowest in the latter (90-98). There are, however, some exceptional points outside this general

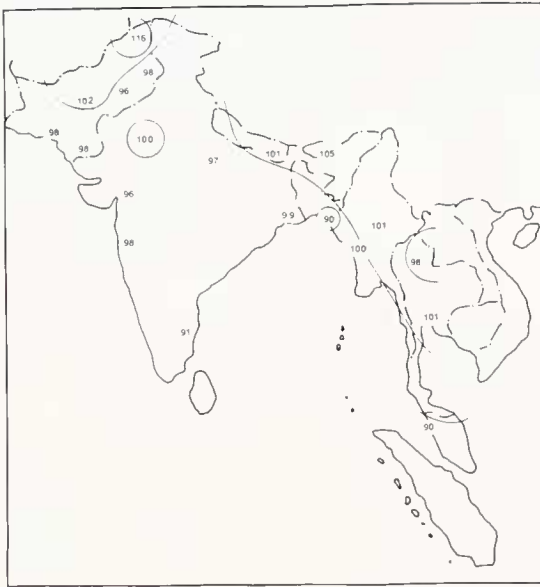


FIG. 8. Geographic variation in the mean angle of the dorsal scale rows.

trend, particularly within Pakistan. Thus the values for the Kirthar, Dadu, Rajasthan samples are significantly lower than all the surrounding ones (t values 2.56 to 4.60, p 0.02 to 0.001). The differences between the the Khuzdar-Quetta samples and Khuzdar-Panjgur samples are not significant. In the eastern sector, the Penang sample has a significantly higher mean angle of the dorsal scale rows (with Rangoon t 3.06 p 0.01; with Thailand t 4.20, p <0.001). The Madras sample is also significantly different from that from Bombay (t 4.01 p <0.001).

Head and Body Length (SVL). —In a short discussion of SVL, Smith (1935) provides data suggesting that the peninsular Indian populations are larger than those of the Indo-Chinese region. Our data confirm this statement, but the larger number of specimens available to us allow a finer-grained breakdown of the size and geographic representation of our sample areas. We find, first of all, that the geographic trends in SVL of males and females parallel one another. Thus, only the males are discussed here (the females follow identical patterns). Adult males from peninsular India and the Indus Valley are significantly larger than those of all

surrounding samples. The mean SVL for the (combined) Indus Valley-peninsular India sample is 94.3 mm. This differs significantly from the combined sample of mountainous Pakistan (Student's t 7.25, p < 0.001, and is significantly different from a combined sample from mountainous India-Nepal (mean 82.1, t 3.32, p < 0.01). The sample from Calcutta has a smaller SVL, but the difference in means is not significant at p < 0.05. However, there is a very significant difference (t 5.6, p < 0.001) between the Calcutta mean (92.2 mm) and that of the combined Myanmar sample (81.2 mm). Samples from Thailand and Malaysia have still lower values, but the means are not significantly different from that of Myanmar at p < 0.05. The calculated differences in the means of all of these samples suggest a broad bi-directional clinal in which the central part of the species range has the highest mean values, with gradually lower ones in all directions, rather than in only one. Analysis of additional samples from peninsular India would undoubtedly clarify the shape of this cline better than we are able to do on the basis of our present material.

What is obvious here is that each of the scale characters analyzed from the standpoint of geographic variation is represented by a different pattern of variation. Thus each of these characters show a pattern of geographic variation that is independent of one another. The patterns undoubtedly reflect the complexity of selective factors acting through the clinally changing physical and/or biotic environments found throughout the species range.

Sexual Variation

As stated above, within all samples examined, males attain a greater SVL than females (though statistically not significant in one, see Table 1). Overall SVL range of all mature males is 70-138, mean 99.3 + 17.2, females 64-121, mean 80.5 + 15.7; Student's t test for difference in means = 5.6, df 264, p < 0.001. Our analysis also shows that this dimorphism is geographically variable (Table 1), with the

TABLE 1. Geographic variation in SVL of adult *Calotes versicolor*.

Sample Area	O.R	Mean	t Test	Probability
Mts. Pakistan				
Males	70-114	81.2	1.93	not sig.
Females	64-79	72.3		
Penin. India				
Males	76-138	102.3	4.20	< 0.001
Females	57-121	86.5		
Myanmar				
Males	71-91	76.9	2.14	< 0.05
Females	68-83	72.2		
Thailand				
Males	73-96	81.4	2.05	0.05
Females	67-88	76.8		

strongest divergence in the peninsular Indian sample.

In a recent morphological study of Tamil Nadu, India samples, Tiwari and Aurofilio (1990) report no sexual difference in scalation. While we find this to be true of almost all of the scale characters we studied, we do find significantly different means in the number of midbody scale rows, with females having a higher number than males by a factor of from 9.7 to 11.7 percent. (six of our largest samples were analyzed; mean in males $41.8 + 9.7$ to $46.7 + 11.1$; females $46.7 + 3.1$ to $48.1 + 9.9$; t 3.5 to 19.5, $p < 0.05$ to < 0.01).

Many workers have described the difference in color and pattern of adult male and female *Calotes versicolor*. In general, the male is lighter, with no, or 4-8 very dim crossbars on the dorsal part of the body. The ground color is usually some shade of tan in the Indian subcontinent and more grayish in the eastern sectors. Adult females are darker, the ground color being brownish to grayish, with the same number, but more obvious narrow brown to black crossbars (or remnants of them).

There is often a faint to quite obvious lighter dorso-lateral stripe on each side of the body. These are missing in adult males. Females usually have a series of circumorbital radiating darker bars which are usually lacking in males. Females lack a dark ventral partial collar at the base of the neck, which is characteristic of the adult males of some populations. Finally, adult males have a remarkable change in color and pattern during the breeding season, which is absent in the females.

Ontogenetic Variation

Ontogenetic variation is noted in color and pattern. The belly of juveniles (< 75 mm SVL) possess 5 to 7, dim, longitudinal, grayish stripes or dashes, each one scale wide. These disappear with age, though they are usually represented in the adult by traces of the median member. In neonates the chin is white to dirty gray, laterally streaked in the sub-infralabial area with a series of medium gray to black diagonal stripes, which become dimmer with age. In one-third- to one-half- grown individuals the chin is additionally suffused with light pink. A series of gray to black

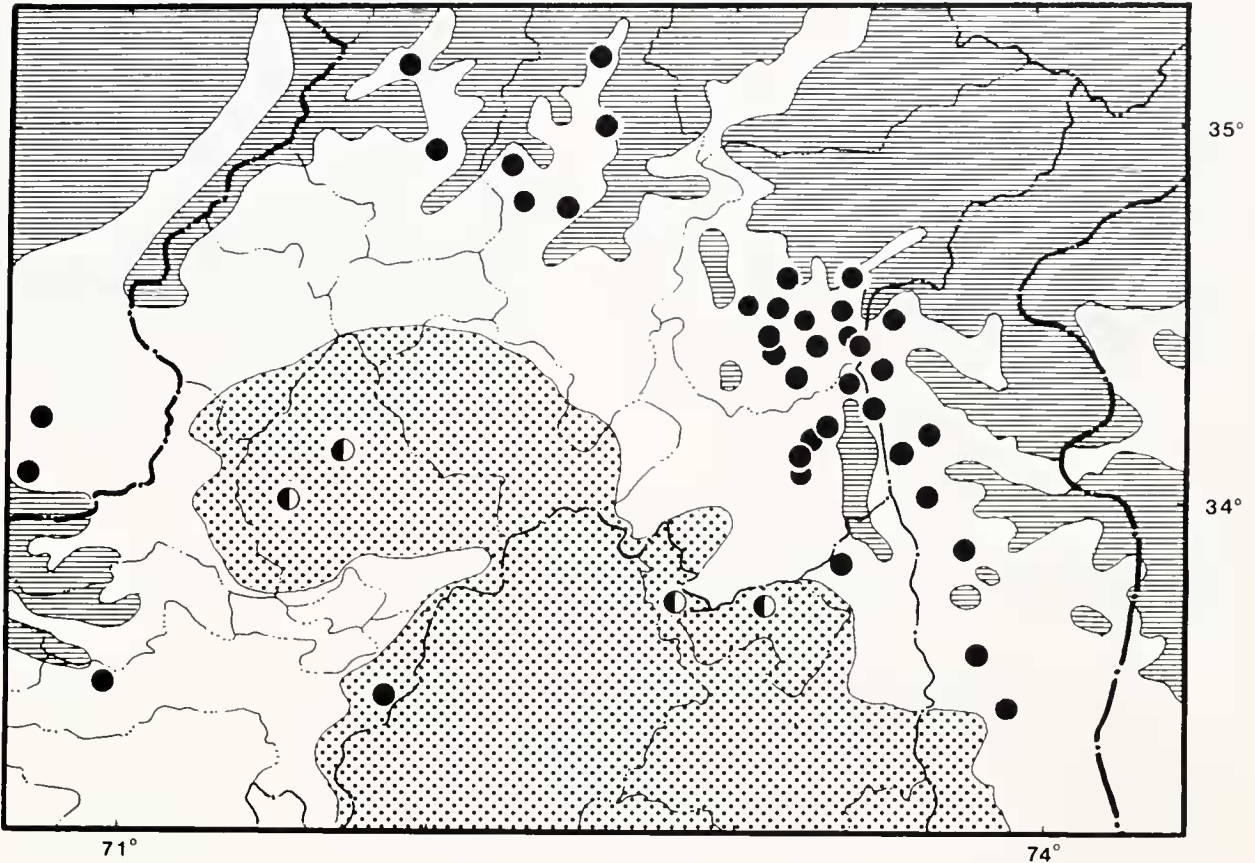


FIG. 9. The geographic distribution of *Calotes versicolor nigrigularis* (solid dots) is restricted to elevations between 300 and 1800 m. The stippled zone is < 300 m, and the cross-hatched one is > 1800 m. Localities of specimens morphologically intermediate between this race and *Calotes v. versicolor* are indicated as half-circles..

radiating circumorbital bars are almost always evident, which also fade with age.

Taxonomic Considerations

This report recognizes a subspecies if 75 percent of the available individuals from a geographic area can be correctly assigned to that provenance on the basis of one or more characters. Analysis of the data suggests that *Calotes versicolor* is divisible into at least two subspecies. Geographic discontinuities in the diagnostic characters are the basis for the generalized racial distributions shown in Figure 9.

Calotes versicolor versicolor (Daudin)

Agama versicolor Daudin 1802:395. Type locality "India".

Agama tiedmanni Kuhl 1820:109. Type

locality Pondicherry, India.

Calotes versicolor (Daudin), Jerdon 1853:470.

? *Calotes viridis* Gray 1846:648. Type locality Madras. (Type specimen lost).

A subspecies of *C. versicolor* distributed from Sri Lanka north through most of peninsular India and Pakistan, west to the Kabul Valley in southeastern Afghanistan, northeast to Hainan Island, China and southeast to Sumatra, Indonesia; replaced in the northern mountains of Pakistan and adjacent Afghanistan and India by *C. v. nigrigularis* (nov. ssp, described below). Other undescribed races probably replace this plains form in northeastern India, and lowland areas of Myanmar, Thailand, Malaysia and Sumatra.

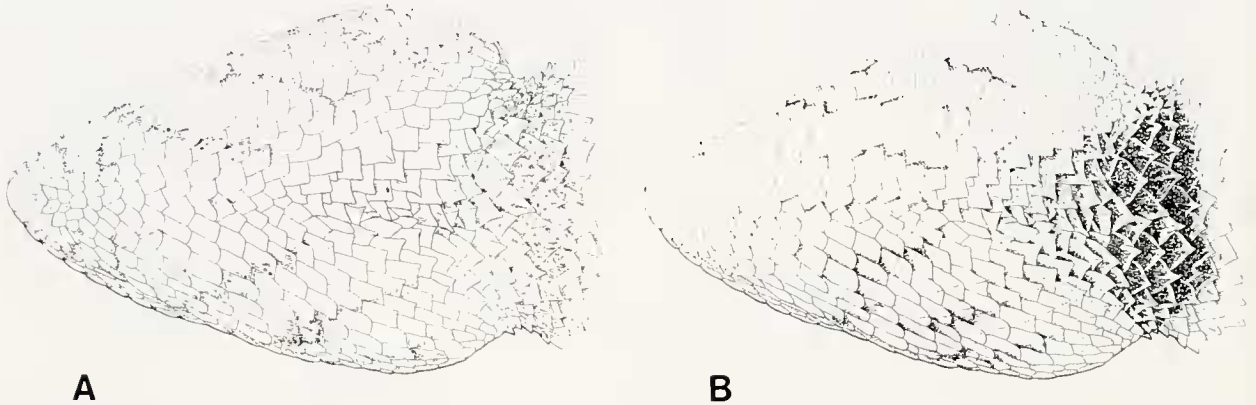


FIG. 10. Chin and throat color pattern in adult *Calotes v. versicolor*. A, FMNH/UF 70511, adult male, Karachi, Karachi Dist., Sindh Prov., Pakistan. B, FMNH/UF 19952, adult male, 8 mi. W. Madras, Tamil Nadu State, India.

C. v. vesicolor has the following suite of characters which distinguishes it from *C. v. nigrigularis*: larger adult size, mean angle of dorsal scale rows $90 - 105^{\circ}$, mean number two distinct postocular stripes (absent in largest males, Fig. 10A), dorsal body pattern usually indistinct, tending to uniform tan during most of the year, becoming pink to reddish in males during the breeding season; 5-7 crossbars may be present (particularly in juveniles and adult females), each 1-2 scales long at the vertebral line; gulars either uniformly light-colored or marked with narrow, diagonal, faint, dusky or sometimes black stripes; scales of the throat and pre-shoulder areas vary from the same color as the gulars to having dark brown or black bases. Large males from southern India often have a ventrally located black, partial collar (Fig. 11); the belly is always uniformly yellowish- to dirty-white.

Several months before the breeding season, the color and pattern of adult males change. At this time the lateral and dorsal surfaces of the head, neck, and shoulders, and the sides of the body all become suffused with yellow, pink, orange, or even dull red (depending on geographic location, and age of the individual). The throat and chest change to orange or red with black mottling (seasonal adult color changes in Indian subcontinent populations

also described by Murray 1886, Smith 1935, and Minton 1966); the tail and limbs become black.

Holotype — Presumably in the Paris Museum, but now lost. The type locality had been simply stated as "India", but this was later restricted to Pondicherry, India by Kuhl (1820).

Exemplary Material Examined.—The specimen materials examined by us that best fit the type description are listed below. We do not include any specimens here from the eastern Himalaya Mountains and from West Bengal eastward, as we believe that those populations will eventually be recognized as representing one or more races distinct from the nominate form and that one described below: FMNH/UF 19886, 19955-9, Kanheri Caves, nr. Borivli, Maharashtra State, India; FMNH/UF 70535-7, Khadiji Falls, Dadu Dist., Sindh Prov., Pakistan; FMNH/UF 19949-53, 8 mi. W. Madras, Tamil Nadu State, India; FMNH/UF 79087, 79099, Sujabad, Deri Ghazi Khan Dist., Punjab Prov., Pakistan; FMNH/UF 78932, Sonmiani, Las Bela Dist., Baluchistan Prov., Pakistan; AMNH 39377-8, 5 mi. E. Kalka and AMNH 39382, nr. Kalka, Amballa Dist., Punjab State, India; CAS 94337-8, 3 mi. SE Sirohi, Rajasthan State, India; MCZ 55502-3, Baroda, Gujarat

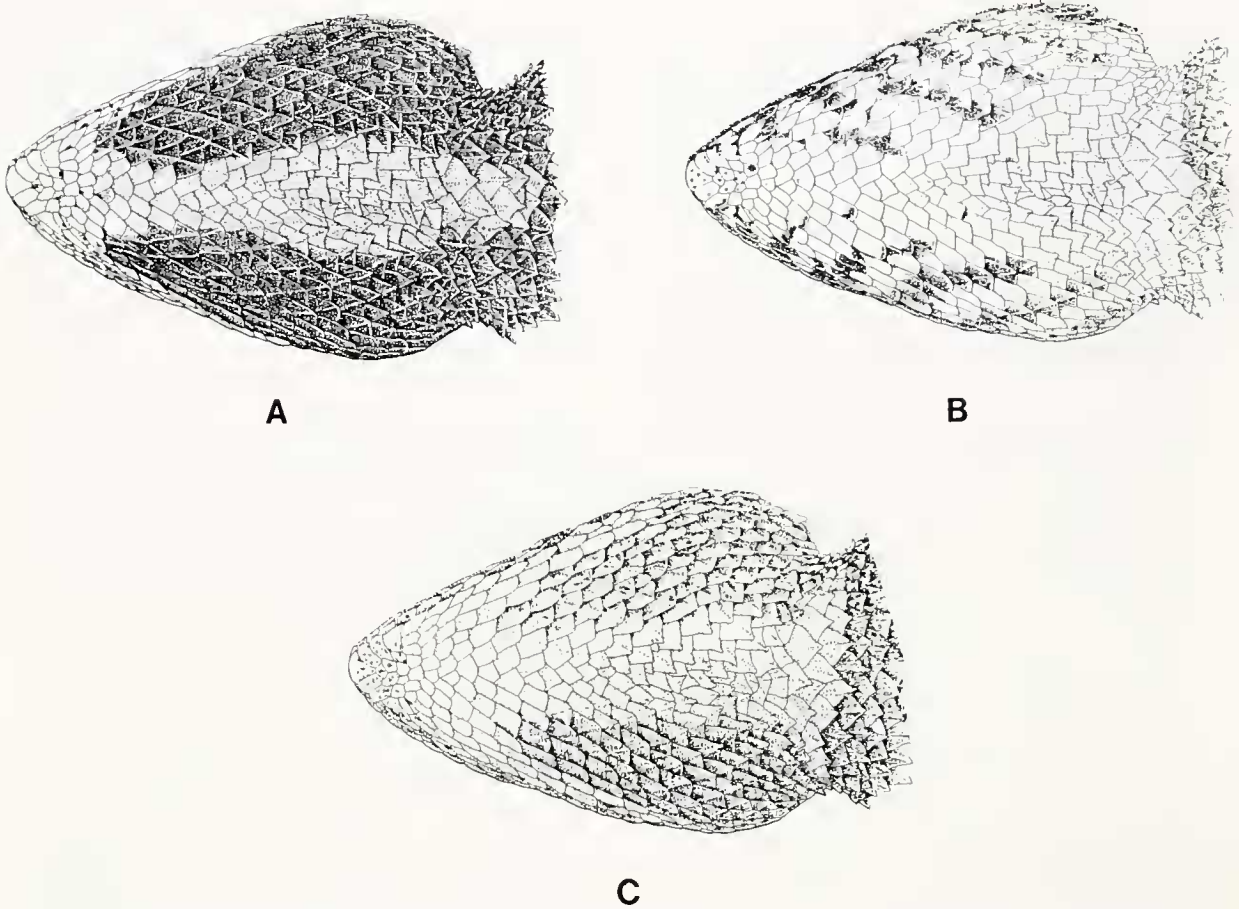


FIG. 11. Chin and throat color pattern in *Calotes v. nigrigularis*. A, FMNH/UF 79470, adult male, nr. Chergal, Manshera Dist., NWFP, Pakistan. B, FMNH/UF, juvenile male, Miandam, Swat Dist., NWFP, Pakistan. C, FMNH/UF 70503, adult female, Abbottabad, Abbottabad Dist., NWFP, Pakistan.

State, India; FMNH/UF 19884-5, New Delhi, India; FMNH/UF 78420, Multan, Multan Dist., Punjab Prov., Pakistan; ZSI 20798, 20800, Pali, Pali Dist., Rajasthan State, India; ZSI 1383, 13486, Ajmer, Rajasthan State, India; ZSI 20796, Jodhpur, Rajasthan State, India; BNHS 325-6, Wanothi, Kutch Dist., Gujarat State, India; BNHS 318 Bhavnagar, Rajkot Dist., Gujarat State, India; SMF 70074 Amritsar, Punjab State, India; SMF 61925, Bangalore, Karnataka State, India; SMF 55444, Meerut, Uttar Pradesh State, India; UMMZ 172083-90, Bhubaneswar, Orissa State, India; and BMNH 1923-3-445, Mirpur Sakro, Thatta Dist., Sindh State, Pakistan.

Scutellation Characteristics.—Overall ranges and means for the scale characters of the samples of *Calotes v. versicolor* examined are as follows (Details regarding

geographic variation in these parameters are found in the diagnosis above, in Figures 5-8, and in the text discussions regarding them): Upper head scales unequal, smooth to feebly keeled; two well-separated spines on each side of the back of the head above the tympanum; canthus and superciliary ridge sharp; 11-13 (mean 12.0) infra- and 11-15 (mean 12.3) supralabials; dorsal scales large, distinctly keeled, all pointing backwards and upwards, larger than the ventral scales, which are always strongly keeled and mucronate, in 35-52 scale rows at midbody (mean 44.5); subdigital laminae of 4th toe 20 - 27 (mean 23.1); gular scales behind mental to middle of eye 7 to 15 (mean 11.2).

SVL and Color Variation.—Juveniles have a dorsal color pattern like that of adult females, except that the ground color is grayish, rather than the usual brownish,

and the dorso-lateral stripes are usually dirty white, rather than yellow. The chin and throat are the same color and pattern as in adult females, except that the lateral black diagonal stripes are usually better defined (Fig. 11).

Nomenclature.—The type localities of both *C. vultuosa* Harlan (1825) and *C. gigas* Blyth (1853) (synonyms of *Calotes versicolor*) are Calcutta, West Bengal, India. Our studies show that *C. versicolor* from West Bengal exhibit a high level of character variation. They are excluded from our synonymy of *C. v. versicolor* on the basis that we cannot confidently place them in any named valid race at the present time, as they are intermediate between surrounding populations in many respects.

Murray (1886) reported *Calotes viridis* Gray (1846) from Upper Sindh, Baluchistan, Punjab, southern India and the Deccan Plateau (this reference not included in *C. versicolor* synonymy given by Smith 1935). Murray's identification of some material from southern Pakistan as *C. viridis* is clearly incorrect, for no specimens referable to this name have been found there by any of the several thorough herpetologists who have worked extensively in Sindh Province since that time. The species has been considered a probable synonym of *C. versicolor*; the species type locality is Madras; the type specimen is lost.

Because the original type locality of *Calotes versicolor* was imprecise, ("India"), Kuhl (1820) re-designated it as Pondicherry, India. It then follows that the peninsular Indian and Indus Valley (*sensu latu*) populations are to be given the name *Calotes versicolor versicolor*. In addition, we note an apparently distinct population of *C. versicolor* which occurs from Thailand, Myanmar, Assam, Sikkim, Darjeeling, and Nepal. However, we believe that taxonomic recognition of this population is not currently warranted until sample sizes are increased and fresher material becomes available for study. Specimens from this area differ from *C. v. versicolor* in having more mucronate dorsal scales, a lower

number of scales under the fourth toe, a higher number of gular scales, wider body crossbands, in having many adults and subadults (in addition to in juveniles) with dusky longitudinal stripes on the belly, and the adults having a smaller SVL. Specimens we recognize as intermediate between these populations and those typical of *Calotes v. versicolor* occur in parts of Nepal and West Bengal.

Geographic and Vertical Range.—*Calotes v. versicolor* does not occur above 2000 m in the Indian Ghats (this study). Populations from the Himalaya Mountains (racially not yet defined), from Garwhal, India east through Sikkim and Bhutan are found to 2500 m elevation (this study), but to only 1030 m in Indochina (Smith 1935).

Calotes v. versicolor (sensu latu) is distributed from the drier, more open forests of Sumatra and the Malay Peninsula north to near Hong Kong and Hainan, west through the mainland to southeastern Afghanistan, and eastern Iran, including the Andaman Islands and Sri Lanka. Additional study will undoubtedly lead to the recognition of additional races in the eastern parts of the range as here defined. If so, the nominate form *C. v. versicolor* will undoubtedly become restricted to those populations living in the lowlands of the Indo-Pakistan subcontinent.

Calotes versicolor nigrigularis ssp. nov.

Holotype.—FMNH/UF 79470 (Figs. 11, 12), adult male, on shrub on rocky hillside, Shargal, 20 km S Balakot, Manshera Dist., Northwest Frontier Province (lat. 34.3° N, long. 73.4° E), Pakistan. Pakistan Museum Natural Science field crew, June 15, 1990.

Paratypes (N 16, all from Pakistan).—AZAD KASHMIR PROVINCE: FMNH/UF 79049, Gulpur; Kotli Dist., FMNH/UF 79396, 81165, Red Fort, Muzaffarabad, Muzaffarabad Dist.; FMNH/UF 79472, Chalpani, Muzaffarabad Dist.; FMNH/UF 79494, Panyola, Poonch Dist.; FMNH/UF 79495,

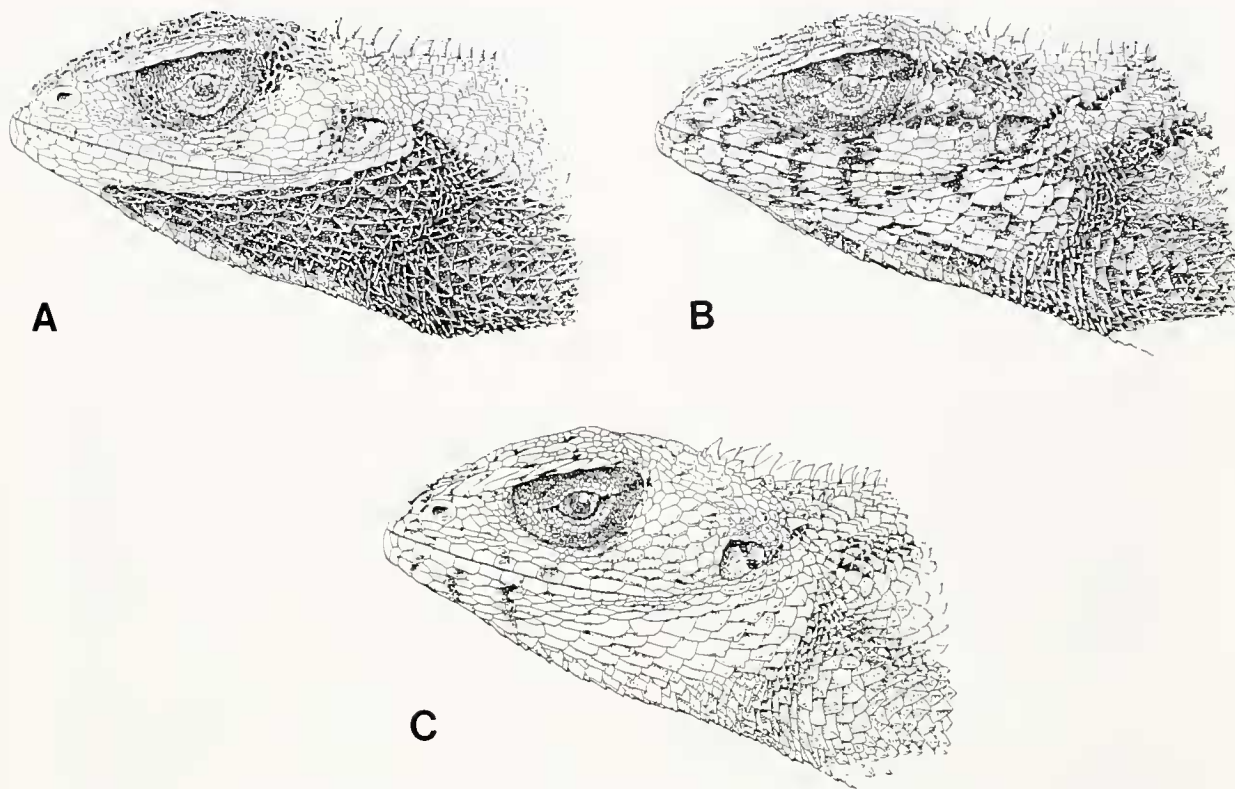


FIG. 12. Side views of head of adult *Calotes versicolor*. A, *C. v. nigrigularis*, FMNH/U 79470, adult male, Chergal, Manshera Dist., NWFP, Pakistan.. B, *Calotes v. versicolor*, FMNH/UF 78926, adult male, Mach, Quetta Dist., Baluchistan, Pakistan. C, *C. v. versicolor*, FMNH/UF 70516, adult male, Karachi, Karachi Dist., Sindh Prov., Pakistan.

Seri, Muzaffarabad Dist.; FMNH/UF 79601, Chela, Muzaffarabad Dist.; NORTHWEST FRONTIER PROVINCE: FMNH/UF 78944, Charsadda, Mandan Dist.; FMNH/UF 79229, Bahrain, Swat Dist.; FMNH/UF 79326, Miandam, Swat Dist.; FMNH/UF 79471 Khakai, Manshera Dist.; FMNH/UF 81133, 11 km W. Hungu, Togh Serai, Kohat Dist.; FMNH/UF 82243, Temargarh, Dir Dist.; FMNH/UF 70503, Abbottabad, Abbottabad Dist.; FMNH/UF 79462 Dhariyal, 4 km SW Balakot. PUNJAB PROVINCE: FMNH/UF 81136, Company Bagh, N. Tret, Rawalpindi Dist.; FMNH/UF 82242, 1.9 km SE Kohala, Rawalpindi Dist.

Other exemplary material (all juveniles, or in poor condition): AZAD KASHMIR: FMNH/UF 82244, Pottri, nr. Bhimber, Mirpur Dist.; PUNJAB PROVINCE: ZSD 1231, Ghora Gali, Rawalpindi Dist.;

FMNH/UF 82656, 11 km S Kohala, Rawalpindi Dist.; NORTHWEST FRONTIER PROV.: FMNH/UF 79138, Miandam, Swat Dist.; BNHS 313, Drosh, Chitral Dist.; FMNH/UF 82821, 1.1 km SW Garh Habibullah, Manshera Dist.; FMNH/UF 82822, 0.6 km SW Garh Habibullah, Manshera Dist.; BNHS 341, Parachinar, Kuram Dist.; FMNH/UF 81218, 13 km NE Abbottabad, Manshera Dist.; FMNH/UF 81093, 2 km W Hungu, Kohat Dist.; and FMNH/UF 82077, 5.8 km NW Khaki, Manshera Dist.

Diagnosis.—Conspecific with *Calotes versicolor* on the basis of its short head, the scales on the sides of the body pointing upwards and backwards, and that it lacks a fold or pit in front of the shoulder. It differs from the nominate race in having more strongly keeled (and usually more mucronate) body scales, more transverse scale rows at midbody, generally more

median gular scales from the tip of the jaw behind the mental to a level perpendicular to the middle of the eyes, fewer enlarged vertebral scales composing the in the nucho-dorsal crest, and in the adult state it lacks dark postocular stripes. During the breeding season the skin over the posterior part of the lower jaw in adult males (only) is jet black, except for a longitudinal median ventral band, which varies with season from pink to scarlet. The most vivid red color is found in the largest males during July and August. Each black gular patch extends (during the breeding season) posteriorly along the side of the neck, thence dorso-posteriorly at an upward angle to the vertebral line, including the entire shoulder region (Figs. 10, 12A). At the same time the entire head and dorsal neck surface are pinkish-red. In some individuals, both the red and black pattern may disappear at death.

Adult males of this race lack the greatly swollen jaw muscle mass of the nominate form, resulting in a head that in top view has more parallel posterior borders behind the eyes than that of *C. v. versicolor* (where these edges are clearly divergent). In many individuals the toes are shorter than in those of the nominate population and the brachium is usually as long as the antibrachium; in *C. v. versicolor* the antibrachium is often shorter.

Description of the Holotype.—Length of the head 1.48 times its width; snout broad, a little longer than the orbit; top of head from side slightly convex, slightly concave from the front; upper head scales unequal, smooth, to faintly keeled or tuberculate; canthus rostralis and supraciliary ridge sharp; two thin, spinous scales above the tympanum, the anterior one smallest, separated from the tympanum by about 5 scale rows; 13 supra- and infralabials; body somewhat compressed laterally; dorsal scales medium in size, distinctly keeled, most being mucronate, pointing backwards and upwards, larger than the ventrals, which are more strongly keeled and mucronate; 51 scales round the middle of the body. No gular pouch; gular scales like those of the ventrals, but larger. Nuchal

and dorsal crests developed, composed anteriorly of lanceolate spines, gradually decreasing in size to the base of the tail. Limbs moderate; fingers 3 and 4 almost equal in length; toe 4 longer than 3. Tail rounded, covered with more or less equal-sized, strongly keeled, mucronate scales.

The measurements (in mm) are as follows: total length 339; SVL 94; tail length 245; body length (axilla-groin) 47; greatest head length (snout tip to posterior extent of lower jaw) 34; greatest head width (across most posterior part of lower jaw) 23; greatest head height (just behind posterior edge of eye) 18.5; height of ear opening 3.1; length of brachium (axilla to elbow) 15; length of antibrachium (elbow to wrist) 13.6; posterior limb when extending anteriorly nearly reaches posterior edge of eye.

The dorsal ground color is more or less grayish-tan (pinkish-tan in life) over the posterior 2/3 of the body. From the level of the posteriorly extended elbows to and onto the base of the tail. The body is very indistinctly marked with 3 slightly darker cross bars. Anteriorly it is almost completely black, being lightest along the vertebral line. Ventrally it is dark gray from near a line connecting the anterior edges of the shoulder posteriorly to just before the insertion of the hind limbs, where the color changes abruptly to grayish cream. The hind limbs and tail base are more or less uniform above and below, matching the colors of adjacent body surfaces. On the dorsal caudal surface, from about the level of the posteriorly adpressed knee to slightly beyond the claw tips of the hind foot, faint darker cross bars can be discerned, fading posteriorly as the tail becomes suffused with dark gray from its middle to the tip. The front limbs from shoulder to claw tips are uniform grayish black. The sides of the neck are black, continuing anteriorly to the black color of the limbs and the sides of the body. The most intense black on the entire individual occurs from the anterior lateral surface of the neck anteriorly onto the jaws and gular region. This black jaw marking is distinctly set off from the lighter color of

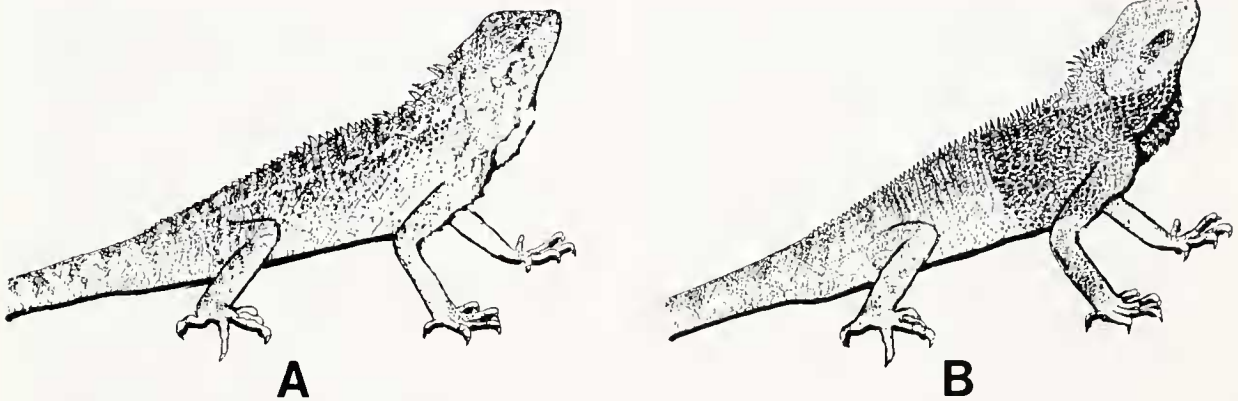


FIG. 13. General body color pattern of *Calotes v. nigrigularis*; A, adult female; B, adult male in breeding coloration.

the head and midgular areas, forming a more or less arrow-shaped black patch on each side (Fig. 10, 12A). Between the two black jaw patches is a dark pink (scarlet in life) median longitudinal band, beginning in the postmental region and extending onto the gular fold. The top of the head is medium gray, slightly mottled with grayish-tan. Laterally and posteriorly this fades into a pinkish-tan which covers all of the temporal areas and extends posteriorly in a V-shaped mark to above the shoulders. The eyelids above and below are light gray, with a nearly black spot in the anterior corner and a larger one in the posterior corner. Both the supra- and infralabials are light grayish-tan with faint grayish stripes radiating from the orbit. The lightest part of the body is in the area of the mental and surrounding shields. The most striking part of the entire color scheme is the black and scarlet gular pattern.

Sex and Color Variation.—Adult females lack distinct metachroic color changes (Fig. 13). The dominant dorsal color is gray to grayish-brown, usually with a narrow white to yellow dorsolateral stripe (sometimes represented by a series of dashes) from the neck to above the hind limb insertion. All these markings are variable in intensity and completeness. Along the vertebral area between the light stripes are 5 to 6 darker brown to black blotches or crossbands, 4 to 5 scales long, which in the largest females fade into the ground color. The ground color of the

gular region is white or pale gray to pink (latter during the breeding season only). There are no large jet-black gular patches as found in adult males, though the base of the scales in this area may be dark gray (Fig. 11). Frequently the gular area is also marked with 5 to 7 more or less distinct black lines or dashes running postero-medially from the infralabials toward the midline.

The reddish throat of adult males is first evident in individuals about 50 mm SVL (FMNH/UF 82656), i.e., at the end of the first year of life. The ventral surface of neonates of both sexes (mean ca 37 mm SVL), through nearly the entire first year is uniform dirty white. The smallest male with well defined black jowls with a red median area has a SVL of 76 mm (FMNH/UF 82623).

Distribution.—This subspecies is restricted to the foothills and outliers of the Himalaya Mountains, from the Jhellum and Neelam River Valleys of Azad Kashmir, Pakistan, west to the Hindu Kush Mountains and foothills bordering the Kabul River Valley in southeastern Afghanistan, south to include the Safed Koh Range on the Pakistan-Afghanistan border (Fig. 1). It may extend further south to Waziristan or even Quetta, but this will only be proven with fresh material (see below). Within this area the race is apparently restricted to subtropical chir pine (*Pinus roxburghii*) and oak (*Quercus*

incana) forests, which are found at elevations between 1000 and 3000 m, depending on exposure and slope conditions.

Individual character states of the plains race *C. v. versicolor* extend into the foothills along several of the larger rivers. Such changes coincide with the general floral change from the plains into the foothills. The Indus Valley (which further specimens may prove completely divides *C. v. nigrigularis* into isolated eastern and western populations) is an example (see remarks of intergradation under *C. v. versicolor*). Such intergrade populations nearly bisect the mountain range of *C. v. nigrigularis* in the Kabul River Valley near Peshawar (specimens in ZSDP, uncat.). We have not yet found any intermediate populations in the valleys of the Neelum or Jhellum Rivers. However, intergrades do occur near the foot of the Himalayan front range (Taxila and Islamabad, PMNH uncat.). The fact that specimens somewhat intermediate between the two races have been found as far south as Khuzdar, Baluchistan (BMNH H 1964-276-8) suggests that *C. v. nigrigularis* may eventually be found throughout the Quetta area and the Central Brahui Range as well, though no fresh specimens are available for study at this time.

The only other intensive study of geographic variation of character states in Pakistan with which these results can be compared is our earlier study of *Echis carinatus* (Auffenberg and Rehman 1991). Like *Calotes versicolor*, this species is found over virtually all of Pakistan except the higher mountains. *Calotes versicolor* does not, however, occur in the sandy deserts of northwest Pakistan.

In the *Echis* study we analyzed 12 characters. While each of these demonstrate a unique pattern of geographic variation, several features common to most of them stand out. These comprise what we believe to be five major centers of adaptive speciation in *Echis carinatus* - Transcaspiya, Iranian Plateau, Astola Island, Indo-Gangetic Plain, Himalayan foothills,

and the Cholistan-Thar Desert. Of these, the first three are essentially extralimital from the standpoint of the current study. The remaining three areas (Himalayan foothills, Indo-Gangetic Plain and Cholistan-Thar Desert) are also recognizable on the basis of distinctive character states, or combination thereof, in the characteristics of *Calotes versicolor* populations studied in this report. Thus, the Himalaya foothills populations are distinguishable from those of the Indo-Gangetic Plain and Cholistan-Thar Desert on the basis of several significantly different scale characters as well as a strikingly different metachroic color and pattern change in the adult males during the breeding season. Likewise, the Desert populations are different at statistically significant levels from those of all the surrounding Indo-Gangetic Plains populations in regard to certain scale characters. Though the recommended nomenclatorial designation for these *Echis* and *Calotes* populations is different in each case, the correspondence of similar geographic patterns of variation is certainly important from the standpoints of both zoogeography and speciation in the subcontinent.

We have not found any evidence for the curious mosaic of mean character states found in the Indus Delta region, as we did for *Echis carinatus*. The reason may be related to the fact that *Calotes versicolor* is often found in riverain forests, so that river and channel changes may be less important as an isolating mechanism in this species than in *Echis carinatus*.

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- ### APPENDIX 1
- Localities (to district only) from which specimens were examined, the museum collections in which they are found, and the number studied (in parentheses).
- AFGHANISTAN: BMNH (3); Jalalabad CAS (3).
- BANGLADESH: Chittagong MCZ (1).
- INDIA: **Assam State:** Chabus AMNH (1), Goalpara Dist., Raimona FMNH (3); **Behar State:** Benares BMNH (8), Patna BMNH (1); **Gujarat State:** Baroda MCZ (2); Bhaunagar BNHS (1), Hingolghadh BNHS (2) Rajkot BNHS (1), Kutch BNHS (2); **Himachal Pradesh State:** Amballa MCZ (2); Kulu Valley MCZ (2); **Jammu-Kashmir State:** Jammu BMNH (1); **Karnataka State:** Bangalore SMF (1); **Maharashtra State:** AMNH (1), Bombay FMNH/UF (7); **Orissa State:** Bhubaneswar UMMZ (13); **Punjab State:** BMNH (1), Amritsar SMF (1), Amballa Dist. nr. Kalka AMNH (3); **Rajasthan State:** Ajmer ZSI (2), Bikaner ZSD (1), Pali ZSI (1), Jodhpur BNHS (1) CAS (2), SMF (1), ZSI (3) Mt. Abu/Abu Rd. CAS (1), AMNH (1); Nagaur ZSI (2), Jaipur ZSI (4); **Tamil Nadu State:** Madurai FMNH/UF (7); **Uttar Pradesh State:** nr, Chalti BMNH (1), Delhi FMNH/UF (2), Kanpur AMNH (1); Pitharagah (Kumaon) BMNH (1), Meerut SMF (1), Mussoorie ZSI (1); **West Bengal State:** Calcutta UMMZ (1), FMNH (2), MCZ (6), Darjeeling MCZ (1), Kalimpong Dist. Tarkhala MCZ (1).
- HONG KONG: BMNH (3).
- MYANMAR ("Burma"): Rangoon FMNH/UF (27); Arakan FMNH/UF (4); Mandalay FMNH/UF (2); "at Chinese border" BMNH (1).
- MALAYSIA: **Penang State:** Penang FMNH/UF (8).
- NEPAL: BMNH (10), Katmandu SMF (1), Swayabonath SMF (1), Lapha Kamali Valley BMNH (1), Rasna Dist. BMNH (1), Maewa-Khola BMNH(12).
- PAKISTAN: **Azad Kashmir Prov.:** Muzaffarabad Dist. SMF (1), FMNH/UF (5); Kotli Dist. FMNH/UF (2); Poonch Dist. FMNH/UF (1); Mirpur Dist. FMNH/UF (2); **Baluchistan Prov.:** Kalat Dist., AMNH (1), BMNH (2), ZSI (1); Las Bela Dist. AMNH (4), FMNH/UF (2); Panjgur Dist., MCZ (1); Quetta Dist. FMNH/UF (1); Khuzdar Dist. BMNH (3); Waziristan Dist. BNHS (1); **Northwest Frontier:** Chitral Dist. BNHS (1); Dir Dist. FMNH/UF (1); Abbottabad Dist. ZSD (1), FMNH/UF (1); Kohat Dist. FMNH/UF (1); Kuram Dist. BNHS (1); Manshera Dist. ZSD (2), FMNH/UF (7); Peshawar Dist. BNHS (1), ZSDP (3), Swat Dist. FMNH/UF (6); **Punjab Prov.:** Dera Ghazi Khan Dist. FMNH/UF (2); Lahore Dist. ZSI (1); Kohat Dist. FMNH/UF (1); Multan Dist. ZSDM (4), FMNH/UF (1); Chakwal Dist. ZSI (2); Bahawalpur Dist. ZSDM (3); Rawalpindi Dist. ZSD (1), CAS (1), FMNH/UF (3); **Sindh Prov.:** FMNH (1); Badin Dist. ZSD (1); Dadu Dist. AMNH (1), ZSD (1), FMNH/UF (4); Hyderabad Dist. AMNH (7), BMNH (1), ZSD (1); Karachi Dist. AMNH (4), BMNH (4), CAS (7), FMNH (4), UMMZ (4), SDSNH (1), FMNH/UF (91), ZSD (30), ZSI (2); Thatta Dist. AMNH (7), UMMZ (1), ZSD (6), FMNH/UF (2); Thar Parkar Dist. BNHS (1), ZSD (2).
- REPUBLIC OF THE MALDIVE ISLANDS: Addu Atoll BMNH (2), Baras Isl. BMNH (1); Hulalag Isl. Bmnh (3); RAF Base BMNH (1).

SIKKIM: BMNH (1); Mangpu FMNH (34),
Teesta Valley MCZ (2).

THAILAND: **Bangkok Prov.:** FMNH/UF (2);
Chiang Mae Prov.: FMNH/UF (5); **Mae
Hong Son Prov.:** FMNH/UF (1); **Udon
Thani Prov.:** FMNH/UF (1); **Yala Prov.:**
FMNH/UF (1); **Phattabung Prov.:** FMNH/UF
(1).